

Hyaena hyaena. By Ingo Rieger

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Hyaena Brisson, 1762

Hyaena Brisson, 1762:13 and 168. Type species *Canis hyaena* Linnaeus, 1758, by original designation.

Euhyaena Falconer, in Murchison, 1868:464. Type species *Canis hyaena* Linnaeus, 1758, by original designation.

CONTEXT AND CONTENT. Order Carnivora, Superfamily Feloidea, Family Hyaenidae, Subfamily Hyaeninae. The subfamily includes two genera and three species, *Hyaena hyaena*, *H. brunnea*, and *Crocota crocata*.

Hyaena hyaena (Linnaeus, 1758)

Striped Hyaena

Canis hyaena Linnaeus, 1758:40. Type locality Benna Mountains, Laristan, Southern Persia.

Hyaena striata Zimmermann, 1777:366. Renaming of *hyaena* Linnaeus.

Hyaena dubbah Meyer, 1793:94. Type locality Athara, Anglo-Egyptian Sudan.

Hyaena orientalis Tiedemann, 1808:350. Renaming of *hyaena* Linnaeus.

Hyaena fasciata Thunberg, 1820:59. Renaming of *hyaena* Linnaeus.

Hyaena antiquorum Temminck, 1820:51. Renaming of *hyaena* Linnaeus.

Hyaena vulgaris Desmarest, 1820:215. Type locality "Patrie. La Barbarie, l'Egypte, l'Abyssinie, La Nubie, La Syrie, La Perse."

Canis hyaenomelas Bruce in Desmarest, 1820:215; status of name not clear; from "Abyssinie et de Nubie."

Hyaena dubia Schinz, 1821:509. Type locality Dongola, Sudan.

Hyaena virgata Ogilby, 1839:lxiv. Renaming of *hyaena* Linnaeus.

Hyaena barbara Blainville, 1844:81. Type locality Oran, western Algeria.

Hyaena indica Blainville 1844:82. Renaming of *hyaena* Linnaeus.

Hyaena suilla Filippi, 1853:127. Type locality Gabes, southern Tunisia.

Hyaena syriaca Matschie, 1900:54. Type locality Antiochia, Syria.

Hyaena schillingsi Matschie, 1900:55. Type locality Kilimanjaro, East Africa.

Hyaena zarudnyi Satunin, 1905:7. Type locality Karun River, Iraq.

Hyaena bokharensis Satunin, 1905:8. Type locality Bokhara, Russian Turkestan.

Hyaena bilkiewiczzi Satunin, 1905:9. Type locality Ashabad, Russian Turkestan.

Hyaena bergeri Matschie, 1910:361. Type locality Eljago, Escarpement, Kenya.

Hyaena satunini Matschie, 1910:363. Type locality Caucasus.

Hyaena rendilis Lönnberg, 1912:64. Type locality Guaso Nyiro, Kenya.

Hyaena sultana Pocock, 1934b:636. Type locality Mt. Qara, 1500 ft, Ain, South-Eastern Arabia.

CONTEXT AND CONTENT. Context in generic summary above. In the previous century and the first decades of this century, several subspecies were described, using mainly striation and color patterns for differentiation. Pocock (1934a, 1934b) used cranial measurements and distinguished the following five subspecies:

H. h. barbara Blainville, 1844:81, see above (*suilla* Filippi a synonym).

H. h. dubbah Meyer, 1793:94, see above (*hyaenomelas* Bruce, *dubia* Schinz, *schillingsi* Matschie, *bergeri* Matschie, and *rendilis* Lönnberg are synonyms).

H. h. syriaca Matschie, 1900:54, see above (*zarudnyi* Satunin, *bokharensis* Satunin, *bilkiewiczzi* Satunin, and *satunini* Matschie are synonyms).

H. h. sultana Pocock, 1934b:636, see above.

H. h. hyaena Linnaeus, 1758:40, see above (*striata* Zimmermann, *orientalis* Tiedemann, *fasciata* Thunberg, *antiquorum* Temminck, *vulgaris* Desmarest, *virgata* Ogilby, and *indica* Blainville are synonyms).

Anatomical, behavioral, and ecological data suggest integrating striped hyaena subspecies into two groups, consisting of (1) the larger, northern subspecies *H. h. barbara*, *syriaca*, and *hyaena*, and (2) the smaller, southern subspecies *dubbah* and *sultana* (Rieger, 1979a).

DIAGNOSIS. Members of the genera *Hyaena* and *Proteles* have pointed ears and long hair along the neck, back, and tail (Fig. 1). In *Crocota*, the ears are round and the dorsal mane is not prominent. *Proteles* is the only hyaenid genus with five digits on the forepaws; other genera have four digits. The sexual organs of *Hyaena* and *Proteles* are not specialized as are those of *Crocota* in which the females have penis-like vulvas. *Hyaena* and *Crocota* have powerful jaws and teeth (these are reduced in *Proteles*). The first lower molar has a small metaconid in *Hyaena* but not in *Crocota* (Ewer, 1954a). *Hyaena hyaena* differs from *Hyaena brunnea* in less reduced upper first molar (largest measurement twice or more than that of first premolar), body with distinct stripes, and long hairs in distinct mane rather than more widely distributed on body.

GENERAL CHARACTERS. Hyaenas other than the aardwolf have distinctly carnassial dentitions superficially similar to those of felids, and have well-developed sagittal crests that increase the area for origin of powerful temporal muscles. Hyaenas are digitigrade and have non-retractile claws (Pocock, 1916). Anal glands lead into an anal pouch that can be extruded during scent marking and in other behavioral contexts (Fig. 1). Testes are internal in hyaenas. Hyaenas have 15 or 16 thoracic vertebrae, compared to 13 or 14 in most other carnivores (Ewer, 1973; Flower, 1869).

Striped hyaenas are comparatively large and have a broad head; forequarters are heavier than hindquarters and forelegs are longer than hindlegs. Weights vary from 25 to 55 kg. Lavauden (1926) spoke of hyaena body weights "up to 100 kg," a remark to



FIGURE 1. Striped hyaena, *Hyaena hyaena*, male during scent marking. Note anal pouch. Photo of captive individual, Zurich Zoo, by author.

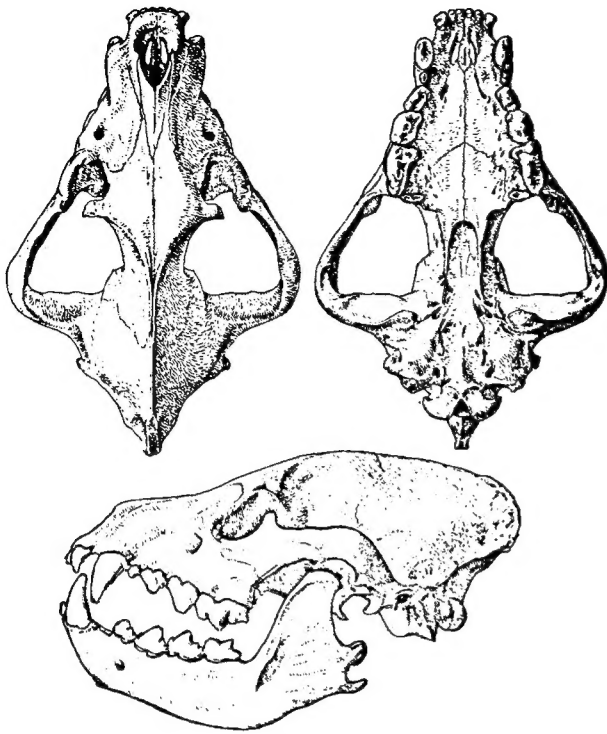


FIGURE 2. Dorsal, ventral, and lateral view of the cranium and lateral view of the left mandible of *Hyaena hyaena*. Adapted from Novikov (1962).

be doubted until measurements confirm it. Total length of striped hyaena skulls (illustrated in Fig. 2) ranges between 220 and 260 mm (mean 240.7, SD 8.9, $n = 63$); zygomatic width ranges between 140 and 170 mm (mean 154.0, SD 6.6, $n = 63$). Neither body weights nor skull measurements indicate any sexual dimorphism in striped hyaenas, which is contrary to results from spotted hyaenas (Matthews, 1939; Kruuk, 1972). Total body length (all measurements in mm) is about 1120 to 1840 (mean 1350, SD 220, $n = 11$), length of tail 265 to 471 (mean 338, SD 55, $n = 19$), length of head and body 1036 to 1190 (mean 1103, SD 52, $n = 13$), and height of shoulder 600 to 942 (mean 814, SD 187, $n = 3$). Pocock (1934a) measured hair length of mane, tail, and flank, which were, respectively, 125 to 250 (mean 184, SD 35, $n = 20$), 75 to 160 (mean 135, SD 22, $n = 20$), 42 to 100 (mean 62, SD 17, $n = 20$). Ear length is about 122 to 152 (mean 139, SD 13, $n = 8$). All body measurements averaged smaller in the two southern subspecies, *H. h. dubbah* and *sultana*, than in the three northern subspecies, *barbara*, *syriaca*, and *hyaena* (Rieger, 1979a).

DISTRIBUTION. The striped hyaena's geographic range extends from North and East Africa through Arabia and Asia Minor to India (Fig. 3). Individuals were seen at 2,250 m above sea level in Persia (Blanford, 1876; Lay, 1967; Ognev, 1962), 2,500 m in India (Anonymous, 1936), and 3,300 m in Pakistan (Roberts, 1977). Over their entire range, striped hyaenas prefer open habitats and sparsely vegetated thorn bush. Desert areas, such as the centers of the Sahara and the Arabian desert are avoided; water must be available within 10 km. In many local areas, striped hyaenas survive only in mountainous retreats. They prefer to retreat into rocky ravines and cave labyrinths (references on this subject reviewed by Rieger, 1979a).

FOSSIL RECORD. Fossil hyaenid specimens date back to the lower Pliocene. Their systematic classification is unclear and so no details are mentioned here. Thenius (1966) reviewed hyaenid evolution and gave many details. *Hyaena* and *Crocota* convergently evolved dentitions with enlarged premolars and simplified or reduced first molars. The oldest postulated direct ancestor of the extinct striped hyaenas, *Hyaena pyrenaica* (Depéret, 1890), was discovered in upper Pliocene deposits in Europe. *Ichtherium*, from the lower Eurasian Pliocene, is thought to be the common ancestor of both living *Hyaena* species (Thenius, 1966, 1969). The geographic range of ancestors of striped hyaenas

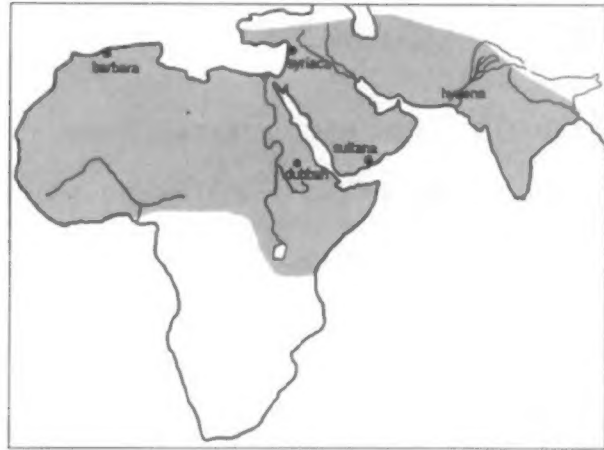


FIGURE 3. Recent range of *Hyaena hyaena*. Dots indicate type localities of the subspecies. Boundaries between ranges of subspecies not precisely known.

was much larger than that of the recent species; fossils are known from Britain and the Pyrenees in the west to Choukoutien in the east; related fossil specimens of a now extinct line were found in the upper Pliocene of South Africa (Ewer, 1954b).

FORM AND FUNCTION. Ducts from the anal glands open into an anal pouch, situated dorsal to the anus. Striped hyaenas extrude this pouch during scent marking and greeting behavior (see Behavior). A striped hyaena can erect its mane and tail hairs. Both *Hyaena* species have throat patches whose coloration differs from that of the surrounding coat. The black throat patch of the striped hyaena has thickened skin and denser fur (Harrison, 1968). Two functions are attributed to this throat patch: camouflage (Kruuk, in litt.) and bite orientation during agonistic interactions (Rieger, 1978). Teat numbers seem to vary individually; some authors speak of two pairs (Grimpe, 1916; Harrison, 1968; Schreber, 1778), others of three pairs (Haltenorth and Diller, 1977; Oken, 1816; Roberts, 1977; Rieger, 1979b). Grimpe (1916) and Rieger (1979b) found that only the two caudal pairs of teats were lactating.

Permanent dentition is i 3/3, c 1/1, p 4/3, m 1/1, total 34; milk dentition is i 3/3, c 1/1, p 4/4.

A baculum is missing in all hyaenid species (Brehm, 1915; Ewer, 1973). The reproductive tract and organs of striped hyaenas are not specialized; however, those of female spotted hyaenas closely resemble those of males (Wells, 1968).

Dilated pupils are round; contracted pupils seem to have different forms. Schneider (1930) described pupils with wider openings at the upper and lower ends that are separated by a narrower connection (confirmed by personal observations).

Coloration and visibility of striation change according to hair length. Thus, marked differences between summer and winter pelts exist. In summer, the striation pattern, due to shorter hair, is clearly visible (Ilany, 1975); the same holds true for hyaena cubs (Rieger, 1979b). The ground color of the pelt is usually gray to light brown. The Lebanese hyaena population is said to have a reddish ground color (Lewis et al., 1968).

ONTOGENY AND REPRODUCTION. Gestation periods, followed by successful rearing of offspring, lasted 90 to 92 days (Rieger, 1979c). Litter size varies from 1 to 5 (mean 2.4). Litters occur throughout the year, but only those born between May and October were successfully reared in captivity (Rieger, 1979c). Body weights of newborn striped hyaenas average about 700 g. A more or less linear increase in weight results in a body weight of about 4 kg at two months of age. Newborn striped hyaenas have ears and eyes closed. By days 5 to 8, the eyes open. At day 8, the cubs start walking. The upper incisors erupt at day 21, and the lower incisors erupt on day 22. At day 24, four incisors are present in the upper and lower jaws, and the hyaena cub starts self-grooming. Urination and defecation without stimulation by the mother are first seen at day 26. At day 30, litter mates start to interact socially with play behaviors. At the same age, cubs are seen to eat meat. Upper canines erupt on day 33. At day 35, ears are no longer folded, but stand erect. The last incisors of the

lower jaw erupt around day 36 (Rieger, 1979b). Ilany (1975) noted that hyaena cubs 4 to 5 months of age were still nursing. Striped hyaenas attain sexual maturity at year 2 or 3 (exceptionally at 18 months) (Rieger, 1979c).

In captivity striped hyaenas show no signs of seasonality in reproduction. Females come into heat any time during the year. Estrus lasts one day (exceptionally two). Post-partum estrus follows 20 to 21 days after birth. Some authors indicate an estrous cycle of 40 to 50 days (reviewed in Rieger, 1979c). During the short estrus several matings, each lasting longer than 10 min, may occur. During copulation, the male is on top of the female, but pelvic thrusts are not observed (Rieger, 1979b).

Longevity under zoo conditions is 23 to 24 years (reviewed in Rieger, 1979a).

ECOLOGY. The small hyaena subspecies of Arabia, *H. h. sultana*, was sympatric with *Crocuta* until recently (Kurtén, 1965, in litt.). The East African subspecies, *H. h. dubbah*, still occurs in the same habitat as the spotted hyaena; observations by Kruuk (1976) indicate that *Crocuta* dominates *H. h. dubbah* there. The same dominance relationship probably prevailed between *sultana* and the now extinct *Crocuta* population in Arabia. In contrast, the three northern striped hyaena subspecies are as large as the spotted hyaena. These northern subspecies, however, have no direct competitors, and several observations suggest that they are able to form small social units and hunt prey animals larger than those of their smaller, southern conspecifics (Ilany, 1975; Kruuk, 1976; Macdonald, 1978).

In his review, Rieger (1979a) demonstrated ecological differences between the northern subspecies, *H. h. barbara*, *syriaca*, and *hyaena*, and the southern subspecies, *dubbah* and *sultana*. Beside being scavengers in every part of their range, the three larger, northern subspecies prey on sheep, goats, dogs, donkeys, and horses. Information on the smaller, southern subspecies is not available. Kruuk (1976) compared the diet of the East African striped hyaena with that of the sympatric and dominant spotted hyaena. He found that *H. h. dubbah* fed on small animals (rodents, birds, reptiles), carrion, and vegetables, whereas the diet of *Crocuta* consisted of large ungulates. A comparatively high amount of the striped hyaena's diet throughout its range consists of vegetables (Flower, 1932; Harrison, 1968; Ilany, 1975; Kruuk, 1976; Macdonald, 1978; Novikov, 1962; Schreber, 1778). Aside from man, striped hyaenas have few regular enemies. Some researchers indicate that Indian striped hyaenas are dominated by adult tigers (Prater, 1948; Sankhala, 1974; Schaller, 1967), whereas the hyaenas dominate the tiger cubs, leopards, and dogs (Anonymous, 1936; Burton, 1931; Champion, 1927, 1933). East African striped hyaenas are at a dominance level equal to leopards (Kruuk, 1976), but they give way to spotted hyaenas and packs of dogs (Heck, 1930; Kruuk, 1976).

Little is known of the land tenure system of striped hyaenas. Evidence reported by Kruuk (1976) and Macdonald (1978) indicates that they have small territories around breeding dens surrounded by large home ranges. Kruuk (1976) gave home range sizes of an East African striped hyaena male and female as 72 km² and 44 km², respectively. Several family groups may use the same area.

Gingerich (1975) and Lydekker (1907) assumed that the aardwolf, which has a pattern of stripes closely resembling that of striped hyaenas, was thus protected from leopard attacks (leopards give way to striped hyaenas). As striped hyaenas and aardwolves are not sympatric over all of their ranges, this hypothesis does not explain why South African aardwolves resemble striped hyaenas that only occur in East and North Africa. Goodhart (1975) gave evidence that aardwolves and striped hyaenas have retained a phylogenetically old cryptic coloration.

The relationship between striped hyaenas and humans has several aspects. In colonial times, Europeans hunted striped hyaenas which "provided really good sport" (Bird, 1946). Usually hyaenas are thought of as cowardly, thus they are not considered to be good trophies (Brehm, 1915; Lydekker, 1907; Ognev, 1962; Sanders, 1931). Sometimes striped hyaenas attack livestock and they may even attack human beings, mainly children (Rieger, 1979a). Natives living within the range of the northern subspecies attribute superstitious functions to various parts of a striped hyaena's body. In India, the tongue is said to reduce dangers from tumors and the fat is believed to cure rheumatism (Prater, 1948). In North Africa, mane hairs have talisman functions (Fitter, 1968) and brain substances are used as aphrodisiac (Lavauden, 1926). Some Egyptians believe that the hyaena heart increases their courage (Prater, 1948). In ancient Egypt, striped hyaenas were tamed and used for hunting purposes; they were

also fattened as a source of food (Roosevelt and Heller, 1914). The latter is still practiced by the North African tuaregs (Lhote, 1946). For entertainment, fights between striped hyaenas and dogs are organized in Afghanistan (Naumann and Nogge, 1973).

To capture striped hyaenas, Europeans used heavy traps with baits (Bodenheimer, 1920, 1935; Heck, 1930; Oerzen, 1913), whereas natives in North Africa, Asia Minor, and Afghanistan crawled into a hyaena burrow while murmuring prayers and shackled the animals with little resistance (Danford and Alston, 1880; Kumerlove, 1967; Lavauden, 1926; Naumann and Nogge, 1973). Insufficiently buried human corpses are occasionally dug out and consumed by striped hyaenas (Bodenheimer, 1935; Brehm, 1915; Cuvier, 1849; Ilany, 1975; Linnaeus, 1758; Ognev, 1962; Tristram, 1880).

Population densities of free ranging striped hyaenas are not known, but are undoubtedly low. Because of hunting pressure and destruction of hyaena habitat and natural food sources by man, *Hyaena h. barbara* from North Africa is in danger of extinction (Chapuis, 1961; Goodwin and Holloway, 1972). The species has been protected in Morocco since 1949 (Chapuis, 1961); striped hyaenas are also protected in Iran (Iran Embassy, Berne, in litt.) and the USSR (Bannikov, 1977). In Turkey, striped hyaenas can be hunted all year (Kumerlove, 1970). A similar situation seems to prevail in most other countries in which they occur (questions on this subject which were sent to wildlife authorities of these countries were not answered). Protection is given only in national parks and reserves. Causes of mortality among free living striped hyaenas in Israel were poisoning, being run over along roads, and being shot by soldiers (Ilany, 1975; Mendelssohn, in litt.).

BEHAVIOR. Both free-living and captive striped hyaenas are crepuscular (Kruuk, 1976; Rieger, 1977b). During the daytime, only individuals that know each other well have been seen to lie with their bodies in contact. Usually, two striped hyaenas lie several meters apart. Their position depends on air temperature; on hot days, they lie on their backs, thus exposing their ventral surface to cool their body temperature. On a cold day, solitary striped hyaenas lie in a vertical roll which minimizes the animal's surface and thus helps to maintain its body temperature (Rieger, 1977b). Lying on its flanks is the most frequently seen position of captive animals (Rieger, 1977b); the same behavior of free ranging animals increases their camouflage (Ilany, 1975).

Urination and defecation closely follow one another, thus forming a composite behavioral pattern (Rieger, 1977b).

Striped hyaenas scent mark while extruding their anal pouch, with which they contact a scent marking post (Holzapfel, 1939; Rieger, 1977a). Posts usually consist of stones, tree trunks, grass, or other objects 5 to 30 cm above the ground (Kruuk, 1976; Rieger, 1977a). The anal gland secretion, of a whitish-yellow color, is transferred onto the scent post either by dropping down from the extruded anal pouch, which is held above the post, or by direct contact between anal pouch and scent post (Fig. 1) (Rieger, 1977a). One substance from the anal gland secretion of striped hyaenas was determined as 5-thiomethylpentane-2,3-dione (Wheeler et al., 1975). Striped hyaenas rub scent on their neck, shoulders, and back from that deposited on posts by conspecifics (Rieger, 1977a, 1979d). Scent rubbing is also elicited by carrion and vomit. Greeting behavior consists of sniffing at the nose, mane, and extruded anal pouch of a conspecific (Fox, 1971; Rieger, 1978), or of repeated pawing of the throat of the partner (Macdonald, 1978; Rieger, 1979b). During agonistic behavior, striped hyaenas try to bite the forelegs and throat of a conspecific. Inhibition of agonistic behavior is achieved by turning the back toward the conspecific and sitting down (Rieger, 1978). Depending on its mood, various parts of a hyaena's dorsal mane are erected. A frightened animal erects the whole mane, but not the hair of the tail. An aggressive animal erects mane hairs of the mid-back and neck. With increasing aggressiveness, the tail is also held up and its hair is erected. Tail position also functions in other contexts. A tail held upward indicates aggressive intentions whereas the tail held downward and between the hindlegs is seen in frightened and fleeing animals (Rieger, 1978). Further information on a striped hyaena's mood is indicated by ear position and vocalization. Flattened ears signal a tendency to bite.

Striped hyaenas are relatively silent compared to spotted hyaenas. Several vocalizations are recognized, however, including growling, howling (a cry indicating readiness for copulation in solitary females), whines, and a mother-cub contact vocalization by the female (Rieger, 1978). I have never heard striped hyaenas laughing like spotted hyaenas and neither has Ilany (1975).

Intensive digging behavior by the female precedes birth. Striped hyaena cubs are reared in natural caves or in burrows dug or enlarged by hyaenas. While digging, striped hyaenas prefer to lie on one flank; thus the burrow width is larger than its height (Rieger, 1979b). Skinner (1976) found the same to be true for brown hyaena burrows. Ilany (1975) described an Israeli striped hyaena lair. It had a small opening 0.4 m in diameter. A 4 m tunnel led to a chamber 1.4 m high. From this chamber, five small openings led to smaller cave-chambers. Broken bones were found in all chambers.

Striped hyaenas regularly carry food items into their burrow. Remains of food are scattered in and around the den (Ilany, 1975; Kruuk, 1976). Ilany (1975) interpreted food carrying behavior as an adaptation to avoid competition for food between striped hyaenas and other carnivores (e.g. lion, leopard, wolf). A striped hyaena is not disturbed in its lair by dominant competitors. When excess food is available, striped hyaenas may store the surplus in tall grass or under bushes (Kruuk, 1976). Striped hyaenas typically feed alone. Conspecifics wait a few meters away until the feeding animal is finished (Ilany, 1975) or makes a "circular tour," a circular walk in an area some 25 m in diameter (Macdonald, 1978). The individual distance between feeding striped hyaenas is reduced during cub rearing. When the cubs start eating meat, their mother tears food items into small parts which she drops beside her cubs (Rieger, 1979b).

Striped hyaenas walk long distances in search of carrion and other food. Their normal walking speed ranges from 2 to 10 km/h (Kruuk, 1976; Rieger, 1977b). In captivity, striped hyaenas tend to show stereotypic walking along cage fences (Holzapfel, 1938; Rieger, 1977b).

Social organization of striped hyaenas has not been studied in detail, but Rieger (1979a) collected evidence supporting the assumption that striped hyaenas form family units which endure for several years. Observations by Ilany (1975) and Macdonald (1978) on free ranging animals are in harmony with this assumption. Depending on the available food source, hyaenas forage alone (mainly the two smaller, southern subspecies which eat smaller food items) or as a small group composed of male, female, and offsprings (mainly the three larger, northern subspecies which prey on medium and large sized ungulates). The strong incompatibility between adult females prevents pack formation such as is seen in spotted hyaenas.

GENETICS. The diploid chromosome number is 40 in all hyaenid species (Hsu and Arrighi, 1966; Ewer, 1973). Genetical experiments with striped hyaenas have not been done, as far as I am aware. In zoological gardens, striped hyaenas are sometimes inbred. But brother-sister inbreeding over three generations did not obviously alter fitness (Rieger, 1979c).

REMARKS. Comparisons of hyaenid behavioral ecology may lead to interesting results, mainly because all four hyaena species are able to live in social organizations of variable complexity. The striped hyaena has by far the largest range of any hyaena species and occurs in diverse habitats. Thus, an investigation of the behavioral ecology of this species would suggest ways in which ecological and behavioral parameters influence each other. The first steps for such a task were undertaken by Kruuk (1976) in East Africa and Ilany (1975) and Macdonald (1978) in Israel. Further studies on striped hyaena populations in North Africa and Arabia should be given priority, because the former is in immediate danger of extinction (Goodwin and Holloway, 1972). *H. hyaena* is similar in size to the spotted hyaena, *Crocuta crocuta*, so a comparison would be interesting. The Arabian striped hyaena subspecies lived in prehistoric times in sympatry with a now extinct spotted hyaena population (Kurtén, 1965). It may be possible to learn how *H. h. sultana* changed its behavior by comparing it with that of the East African subspecies *dubbah*, which still lives together with the spotted hyaena.

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